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REVIEW ARTICLE

Microbial remediation of oil-contaminated shorelines: a review

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Abstract

Frequent marine oil spills have led to increasingly serious oil pollution along shorelines. Microbial remediation has become a research hotspot of intertidal oil pollution remediation because of its high efficiency, low cost, environmental friendliness, and simple operation. Many microorganisms are able to convert oil pollutants into non-toxic substances through their growth and metabolism. Microorganisms use enzymes' catalytic activities to degrade oil pollutants. However, microbial remediation efficiency is affected by the properties of the oil pollutants, microbial community, and environmental conditions. Feasible field microbial remediation technologies for oil spill pollution in the shorelines mainly include the addition of high-efficiency oil degrading bacteria (immobilized bacteria), nutrients, biosurfactants, and enzymes. Limitations to the field application of microbial remediation technology mainly include slow start-up, rapid failure, long remediation time, and uncontrolled environmental impact. Improving the environmental adaptability of microbial remediation technology and developing sustainable microbial remediation technology will be the focus of future research. The feasibility of microbial remediation techniques should also be evaluated comprehensively.

Keywords Shorelines · Oil pollution · Microbial remediation · Environmental adaptability · Sustainable microbial remediation

Introduction

With the continuous expansion of the offshore oil drilling, resource exploration, transportation, and other industrial activities, the marine environment and ecosystems have suffered from serious oil pollution (Lee et al. 2015). According to statistics, from 1970 to 2016 there were more than 460 large-scale oil spills (spill amount > 700 tonnes) around the world (ITOPF 2016), with a total oil spill of more than 5.734 million tons, making oil spills the second largest marine disaster after red tides (Garcia-Olivares et al. 2017). Once an ocean oil spill occurs, a large amount of oil spreads making oil spills and invades the whole shorelines rapidly under the action of currents and wind. The oil continuously penetrates into the deep layer via adsorption by shoreline sediments (Bejarano and Michel 2016), resulting in large-scale and persistent oil pollution along the shorelines. For example, in 2010, the Deepwater Horizon (DWH) blowout released 3.19 million barrels (435,000 tons) of crude oil into the Gulf of Mexico, resulting in approximately 22,000 tons of leaked oil settling on the northeastern coastline of the Gulf (Geng et al. 2021). Shorelines are not only buffer regions for the exchange of materials and energy between the sea and land but also habitats for a large number of sea and land animals/microorganisms (Barbier et al. 2011; Wang et al. 2020a). After oil spill accidents, the biodiversity of metazoan small animals and vertebrates significantly decreases (Table 1). In addition, the shorelines undergo frequent dry and wet alternation, which makes it more difficult to remediate. Therefore, once oil spill pollution occurs, it seriously impacts the ecological environment of the shorelines for a long period

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Table 1 Summary of marine oil spill events (oil spill volume, oil type, cleaning, bioremediation methods, ecological impacts, and affected areas)

Oil spill name	Oil spill type	Oil spill volume	Oil cleanup	Bioremediation method used	Affected wild life	Affected areas	References
Amoco Cadiz (1978), Brittany, France	Light Iranian and Arabian crude oil and bunker fuel	68.7 million gallons	Yes	Artificial fertilizers and bacterial cultures	Fauna in subtidal zone and intertidal zone are strongly affected	Subtidal zone and intertidal zone	Conan Dang et al. (2016)
Peck slip (1978), Cabo San Juan, Puerto Rico	Bunker C	11,000 barrels	Yes	No treatment (natural attenuation)	Red mangroves suffered total defoliation and mortality within the most heavily; there was a large reduction in the population of mangrove Tree Crabs and supratidal beach plants	Supratidal zone	Curl et al. (1992)
Ixtoc 1 oil well (1979), Mexican Gulf, Bay of Champeche	IXTOC I crude oil	3,522,400 barrels	Yes	No treatment (natural attenuation)	Depressed density and abundance in samples from the low and middle intertidal zone	Low and middle intertidal zones	Rabalais and Flint (1983)
North cape oil spill (1980), Baffin Island	Venezuelan Lago Medio sweet medium gravity crude oil	45,000 L	Yes	Commercial fertilizer (Fullgjødsel C)	Fish, invertebrates and sea birds are strongly affected	Intertidal zone	Gongora et al. (2022)
Whidbey Island Spill (1983), South end of Whidbey Island, Washington	Bunker fuel oil	119 barrels	Yes	No treatment (natural attenuation)	Extremely high bird mortality rate	Supratidal zone and upper intertidal zone	Curl et al. (1992)
Exxon Valdez oil spill (1989), Gulf of Alaska	Crude oil	10.9 million gallons	Yes	Slow-release (Customblen) and oleophilic (Inipol EAP 22) fertilizers	Sea otters, harbor seals, bald eagles, seabirds, harlequin, ducks, and salmon fish are strongly affected	Intertidal zone	Bragg et al. (1994); Prince and Bragg (1997)
Apex barges (1990), Galveston Bay, Texas	No. 5 oil	16,476 barrels	Yes	Alpha Bio-Sea microbes with a nutrient additive	Shellfish, shrimp, and finned fish died	Marsh area	Hoff (1993)
Seal Beach (1990), California	Crude oil	20 barrels	Yes	Fertilizer Miracle-Gro and 8 pounds of the bioaugmentation product INOC 8162	National fish and wildlife tubes and salt marsh grass (rush and cross grass) are affected	Marsh area	Curl et al. (1992)
Mega Borg (1990), Mexican Gulf, Mexico	Angolan Palanca crude oil	100,000 barrels	Yes	Alpha Bio-Sea microbes with a nutrient additive	There were no reports of oiled wildlife from the incident	Open waters	Curl et al. (1992)

Table 1 (continued)

Oil spill name	Oil spill type	Oil spill volume	Oil cleanup	Bioremediation method used	Affected wild life	Affected areas	References
Exxon Bayway Refinery (1990), Arthur Kill, New York	No. 2 heating oil	13,500 barrels	Yes	Slow-release (Custom-blen)	960 birds (including 296 seagulls), 29 dead muskrats, 1 cotton tailed rabbit, 1 domestic cat, and 9 live diamond backed Terrapin turtles died	Intertidal zone	Hoff (1992)
Arabian Gulf (1991), Persian Gulf, Kuwait	Kuwait crude oil	9,000,000 barrels	Yes	Bioremediation agents	Increased mortality of beach invertebrate; normal Species diversity decreases and returns after 2–3 years; 20,000 birds and thousands of crabs died	Low and middle intertidal zone	Price (1998)
The Prestige oil spill (2002), Coast of Galicia of north-western Spain	heavy fuel no. 2-M100	63,700 tonnes	Yes	oleophilic fertilizer S200	Sea birds, shark, marine mollusks, mussels, octopus, sardines, and sole goose barnacle are strongly affected	Supratidal zone and intertidal zone	Dave and Ghaly (2011)
Deepwater Horizon (2010), Mexican Gulf, Mexico	Crude oil	210 million gallons	Yes	No treatment (natural attenuation)	Aquatic, invertebrates, fish, sea turtles, birds and beach mouse are strongly affected	Subtidal zone and intertidal zone	Bejarano and Michel et al. (2016)

of time (Lv et al. 2020; Zhang et al. 2019a). As such, there is an urgent need for efficient remediation technologies for heavy oil pollution along the shorelines.

Conventional treatments for oil pollution in the shorelines include physical, chemical, and biological remediation approaches (Agarwala and Liu 2015). Among them, chemical remediation is likely to cause secondary pollution, while physical remediation is very expensive and is mainly used in emergency situations (Daccò et al. 2020). In addition, physical and chemical remediation cannot completely degrade the contaminating crude oil (Agarwala and Liu 2015; Daccò et al. 2020; Lim et al. 2016). Therefore, bioremediation offers a more efficient oil pollution treatment approach, with the advantages of safety, high efficiency, economy, simple operation, and no secondary pollution (Daccò et al. 2020; Pi et al. 2015).

Microbial remediation is the process of using microorganisms to degrade, remove, or detoxify pollutants in the environment, in order to restore normal ecosystem function (Megharaj et al. 2011; Ron and Rosenberg 2014). Research on the migration, transformation, and behavior fate of oil pollutants in marine environments has shown that microbial degradation is the most important and fundamental mechanism to achieve the removal of oil pollutants (Fuentes et al. 2014; Lawniczak et al. 2020; Varjani 2017). There are a large number of oil-degrading microorganisms in the natural environment, including bacteria and fungi, as well as a small amount of algae (Prince 2005; Xue et al. 2015). However, although a large number of publications have reported the biodegradation of petroleum hydrocarbons (Fuentes et al. 2014; Ghosal et al. 2016; Kadri et al. 2017; Lawniczak et al. 2020; Prince et al. 2013; Varjani 2017), only a small number have considered the bioremediation of the shorelines.

The present paper review summarizes current knowledge on the ability of microorganisms to degrade petroleum hydrocarbons, taking into account the sources of oil pollutants, distribution of oil pollutants in the shoreline, impact of oil pollutants on the ecological environment of the shoreline, oil degrading microorganisms, microbial metabolism pathway, and key enzymes for biodegradation of petroleum hydrocarbons. Finally, this review discusses factors affecting biodegradation rate and types of microbial remediation technologies, current limitations, and future research directions.

Causes of oil spills

Both natural and anthropogenic factors can cause ocean oil spills. One of the most common natural causes is oil leakage from the ocean seabed or the discharge of oil yielding rocks from the seabed into the ocean ecosystem (Dhaka and Chattopadhyay 2021). Anthropogenic causes are usually accidental and intentional oil spills. Accidental spills may be due to the grounding and collision of ships carrying oil (Exxon Valdez spill, etc.), accidents at offshore oil rigs (Deepwater Horizon oil drilling platform explosion, etc.), and the storage of crude oil and its derivatives. Intentional oil spills are mainly caused by the discharge of untreated wastewater, the release of fuel from service centers, illegal discharge of sewage, and acts of war. Once an ocean oil spill occurs, large amounts of oil can rapidly spread and invade the whole shorelines under the action of tides and waves. This oil continuously penetrates into the deep layer via adsorption by shoreline sediments.

Distribution of shoreline oil pollutants

Oil types

Crude oil is an organic compound composed of saturated hydrocarbons, aromatic hydrocarbons, resins, and asphaltenes (Varjani 2017). Based on the relative contents of these four components, crude oil can be divided into light, medium, and heavy. According to analysis of the 10 largest oil leakage accidents in history, leaked crude oil mainly includes light crude oil and heavy crude oil (Lim et al. 2016). Generally, light crude oil is mainly composed of saturated hydrocarbons and aromatic hydrocarbons, with relatively less resins and asphaltenes, heavy crude oil has higher contents of resins and asphaltenes (Head et al. 2006).

The behavior and degradability of oil pollutants that ultimately reach the shoreline depend on the type and composition of the crude oil. Most of offshore oil platforms produce light crude oil, but the demand for heavy oil and its marine transportation is growing, increasing the risk of shoreline oil pollution with low degradation potential (Martínez-Palou et al. 2011). However, even leakage of light crude oil leads to the deposition of hydrocarbons with low degradability, because weathering occurs during transportation to the coast (Bacosa et al. 2015). In the first few days, light oil may lose nearly half of its mass due to the release of gases, dissolution of water-soluble hydrocarbons, and evaporation of volatile compounds (Liu et al. 2012). Biodegradation of dispersed crude oil in the ocean is relatively fast (with a half-life of several weeks); however, it is usually much slower along the shorelines (Abou Khalil et al. 2022). Therefore, dispersing oil at sea and preventing it from reaching the shorelines may be the most appropriate approach for managing oil spills. Using fine sediments to disperse crude oil may be a promising method (Ji et al. 2023).

Sediment properties

The properties of surface and subsurface shoreline sediments play a major role in the distribution of oil pollutants (Taylor

and Reimer 2008). Compared with fine-grained sediments, coarse sediments typically facilitate deeper oil infiltration. Sediments with sharp edges and/or wide grain size distributions have lower porosity. Beaches can be found of clay (< 4 μm), silt (4 to 60 μm), and sand (60 μm to 2 mm), and/or different combinations of larger aggregates. Some beaches may consist of two or more types of sediments with different properties (Li et al. 2010).

Oil distribution in the shoreline

The shoreline consists of the supratidal zone, intertidal zone (upper, middle, and lower intertidal zone), and subtidal zone. Generally, the upper intertidal zone has the highest amount of oil deposition (based on oil quality per mass of sediment) owing to the significant decline in the groundwater level associated with this location (Boufadel et al. 2019). The mass of oil in the intertidal zone decreases toward the seaward direction (from upper to mid- to lower intertidal zones), because the groundwater level increases. Oil may also reach the supratidal zone (e.g., zone landward of the shoreline) under the action of storm waves (e.g., storm surges) (Abou Khalil et al. 2021a). Once deposited onto the supratidal zone, oil can penetrate sediments and/or be covered by the sediments of subsequent storm waves. However, the concentration of oil deposited into the supratidal zones tends to be lower than that deposited into the intertidal zones. Table 1 summarizes the impact of some marine oil spill accidents on the supratidal zone, the intertidal zone (upper, middle, and lower intertidal zone), and subtidal zone. Additionally, the spilled oil slicks are likely to break into droplets in the subtidal and intertidal zones of the shoreline owing to wave power. The dispersed oil droplets can interact with the sediments to form oil particle aggregates (OPAs) (Ji et al. 2023). Moreover, some sediments can penetrate oil droplets, causing OPAs to decompose into smaller aggregates, making them less likely to settle and greatly enhancing the microbial degradation of petroleum hydrocarbons. Therefore, these findings also highlight the possibility of mineral deposits being used for dispersion.

Impact of oil pollutants on the shoreline ecological environment

Shoreline oil pollutants can cause significant damage to habitats and pose a serious threat to all organisms living along and within the shoreline (Michel et al. 2017). The potential impact of oil pollution on biota varies by species (Bejarano and Michel 2016). Exposure to spilled oil can affect organisms from the outside through the skin or through direct inhalation and ingestion. The animals most affected by oil include seabirds, turtles, and marine mammal (such as sea otters and seals) (Yuewen and Adzigbli 2018).

Coral reefs, mangroves, and swamps are the most sensitive coastal habitats to oil pollutants. These ecosystems provide coastal protection and feeding/nursery resources for many invertebrate and fish. For example, when the intertidal zone experiences low tide, oil floating on the water surface can be directly deposited onto coral habitats (Guzman et al. 2020). Mangroves are trees and shrubs commonly found along the coasts and estuaries of tropical and subtropical regions (Duke 2016). They provide coastal protection for inland areas from strong storms and provide habitats for various mammals, birds, insects, plants, and algae attached to tree roots (Iturbe-Espinoza et al. 2022). When exposed to tidal currents, oil can adhere to the exposed surfaces and roots of mangroves. When suffocated by oil pollution, plants and animals cannot survive in the mangrove ecosystem. Swamps develop in the intertidal zone of muddy shorelines. They are exposed to high tide water and are susceptible to the influence of floating oil (Challenger et al. 2015). Finally, oil pollution disrupts the food web and leads to shoreline erosion, which will seriously affect swamp areas.

Oil degrading microorganisms

Oil-degrading microorganisms were first isolated almost a century ago. To date, 200 types of oil degrading microorganisms in the marine environment have been reported in the literature, including 90 types of bacteria,103 types of fungi, and 23 types of algae (Prince 2005). Table 2 lists the crude oil degradation characteristics of bacteria, most of which are *Proteobacteria*, *Actinobacteria*, and *Firmicutes*. A group of obligate hydrocarbon-degrading γ-*Proteobacteri*a can only use hydrocarbons as their carbon sources for growth and metabolism. Among them, *Alcanivorax* sp., *Oleiphilus* sp., *Oleispira* sp., and *Thalassolituus* sp. obligately degrade saturated hydrocarbons, while *Cycloclasticus* sp. obligately degrade aromatic hydrocarbons. In addition, *Planococcus* sp. is an obligate degrading bacterium of saturated hydrocarbons (Head et al. 2006). For the remediation of oil-contaminated intertidal sediments, *Acinetobacter* sp., *Pseudomonas* sp., and *Bacillus* sp. play important roles in the bioremediation of oil pollutants owing their widespread presence in the environment and extensive ability to degrade hydrocarbons.

Microbial degradation mechanism of oil pollutants

Both aerobic degradation and anaerobic degradation are involved in the biodegradation process of oil pollutants. Between them, aerobic degradation is relatively more common and has rapid reaction speed and strong adaptability to the environment (McGenity 2014).

Table 2 List of bacteria able to grow using hydrocarbons

Phylum	Species	Typical petroleum hydrocarbons	References
Alphaproteobacteria	*Acidocella*	Naphthalene	Dore et al. (2003)
	Agrobacterium	Phenanthrene, fluoranthene, pyrene	Ben et al. (2008)
	Azospirillum	Crude oil	Muratova et al. (2005)
	Beijerinckia	Phenanthrene and naphthalene	Mallick et al. (2011)
	Blastochloris	Toluene	Zengler et al. (1999)
	Brevundimonas	C15–C36 n-alkanes	Li et al. (2016)
	Lutibacterium	Phenanthrene	Chung and King (2001)
	Ochrobactrum	Phenanthrene, hexadecane, pyrene	Chung and King (2001); Mishra and Singh (2012)
	Paracoccus	C6–C28 n-alkanes, pyrene, fluoranthene, benzo[a]pyrene	Teng et al. (2010)
	Sphingomonas	Fluorene, phenanthrene	Zhou et al. (2016)
	Xanthobacter	Propene, benzene, toluene, and phenol	Hirano et al. (2004)
Betaproteobacteria	*Achromobacter*	C12–C27 n-alkanes, anthracene, phenanthrene, pyrene	Deng et al. (2014)
	Acidovorax	Naphthalene, phenanthrene, chrysene, benz[a] anthracene, benzo[a]pyrene	Singleton et al. (2009)
	Alcaligenes	C17–C33 n-alkanes, naphthalene, anthracene, phenanthrene, dibenzothiophene, fluorene, fluoranthene, pyrene, and chrysene	La1 and Khanna (1996)
	Azoarcus	C6–C8 n-alkanes, benzene, toluene, ethylbenzene, xylene	Kaplan and Kitts (2004)
	Burkholderia	C12–C34 n-alkanes, fluorene, phenanthrene, pyrene, fluoranthene, benz[a]anthracene, dibenz[a,h]anthracene	Wu et al. (2011)
	Comamonas	naphthalene, phenanthrene, anthracene	Meyer et al. (1999)
	Dechloromonas	benzene, toluene, ethylbenzene, xylene	Chakraborty et al. (2005)
	Polaromonas	Naphthalene, C5–C12 n-alkanes	Jeon et al. (2004); Scheps et al. (2011)
	Ralstonia	Toluene	Parales et al. (2000)
	Sphaerotilus	Crude oil	Austin et al. (1977)
	Spirillum	Crude oil	Shinoda et al. (2000)
	Thauera	Toluene, alkylbenzenes, C2–C9 n-alkanes	Dubbels et al. (2009); Rabus and Widdel (1995); Shinoda et al. (2004)
Deltaproteobacteria	*Desulfatibacillum*	C8–C23 n-alkanes	Cravo-Laureau et al. (2004)
	Desulfobacterium	C5–C9 n-alkanes	Mohamad Shahimin et al. (2016)
	Desulfobacula	Toluene, p-cresol, 4-hydroxybenzoate, phenylacetate, benzoate	Kim et al. (2014)
	Desulfosarcina	C17–C30 n-alkanes	Kleindienst et al. (2014); Miralles et al. (2007)
	Geobacter	Toluene	Pilloni et al. (2011)

Table 2 (continued)

Phylum	Species	Typical petroleum hydrocarbons	References
Gammaproteobacteria	*Acinetobacter*	C10–C44 n-alkanes, phenanthrene, pyrene, acenaphthene, fluorene, dibenzothiophene	Gao et al. (2006); Ghosal et al. (2013); Thangaraj et al. (2008); Throne-Holst et al. (2006)
	Aeromonas	hexadecane, acenaphthene, fluorene	Alegbeleye et al. (2017a); Ilori et al. (2005)
	Alcanivorax	C10~C44 n-alkanes, branched alkanes	Liu and Shao (2005)
	Alkanindiges	C9–C18 n-alkanes	Sun et al. (2015a)
	Alteromonas	C8–C16 n-alkanes, naphthalene, phenanthrene, anthracene, pyrene	Jin et al. (2012); Kato (1996)
	Azotobacter	naphthalane, acenaphthene, xylene	Thavasi et al. (2006)
	Cycloclasticus	naphthalene, phenanthrene, anthracene, toluene	Dyksterhouse et al. (1995)
	Dyella	C14–C34 n-alkanes, toluene, naphthalene, phenanthrene	Muangchinda et al. (2013)
	Enterobacter	hexadecane, acenaphthene, phenanthrene	Hua et al. (2010); Muangchinda et al. (2013)
	Erwinia	C16 n-alkanes	Pleshakova et al. (2019)
	Klebsiella	C13–C30 n-alkanes, phenanthrene, fluoranthene, pyrene, benzo[a]pyrene	Xu et al. (2016)
	Leclercia	Pyrene	Sarma et al. (2010)
	Leucothrix	Alkanes	Mahmoud and Bagy (2018)
	Luteibacter	Acenaphthene, phenanthrene	Muangchinda et al. (2013)
	Marinobacter	C16~C30 alkanes, naphthalene, phenanthrene, anthracene	Wang and Shao (2012)
	Moraxella	Biphenyl	Stucki and Alexander (1987)
	Neptunomonas	Naphthalene, 2-methylnaphthalene	Hedlund et al. (1999)
	Oleiphilus	n-alkanes, branched alkanes	Golyshin (2002)
	Oleispira	n-alkanes, branched alkanes	Yakimov et al. (2003)
	Pasteurella	Phenanthrene, fluoranthene, pyrene	Šepič et al. (1997)
	Proteus	C8~C36 n-alkanes, pyrene	Ayotamuno et al. (2006)
	Pseudomonas	C12~C34 alkanes, fluorene, phenanthren, fluoranthene, pyrene, benzo[a]pyrene, benz[a]anthracen, dibenz[u,h]anthracene	Wu et al. (2011); Xia et al. (2014)
	Pseudoxanthomonas	n-alkanes, phenanthrene	Nopcharoenkul et al. (2013); Patel et al. (2012)
	Psychrobacter	Aliphatic hydrocarbons	Bacosa et al. (2016)
	Serratia	n-alkanes, cycloalkane, PAHs	Azizan et al. (2020); Xia et al. (2017)
	Stenotrophomonas	C16 n-alkanes, anthracene, phenanthrene, naphthalene, fluorene, yrene, benzo(e)pyrene, benzo(k)fluoranthene	Arulazhagan et al. (2017); Hassanshahian et al. (2013)
	Thalassolituus	C7–C20 n-alkanes	Yakimov et al. (2004)
	Vibrio	C8–C40 n-alkanes, naphthalene, biphenyle, phenanthrene	Radwan et al. (2007)
	Xanthomonas	Phenanthrene, anthracene, fluoranthene, pyrene	Hamann et al. (1999)
	Xylella	Alkanes	McGenity (2019); Santiago et al. (2018)

Table 2 (continued)

Phylum	Species	Typical petroleum hydrocarbons	References
Actinobacteria	*Actinomyces*	Crude oil	Binazadeh et al. (2009)
	Arthrobacter	Saturated hydrocarbons, aromatic hydrocarbons	Chaıneaua et al. (1999)
	Aureobacterium	Dibenzothiophene	El-Gend (2006)
	Brachybacterium	c17 n-alkanes, c18 n-alkanes, fluoranthene, pyrene	Cong Dang et al. (2016)
	Brevibacterium	alkanes, alkenes, cycloalkanes, aromatic hydrocarbons	Uad et al. (2010)
	Clavibacter	C16–C20 n-alkanes, naphthalene	Dore et al. (2003); Tapilatu et al. (2010)
	Corynebacterium	C8–C40 n-alkanes, 2–6-ring PAHs	Gurav et al. (2017)
	Dietzia	C11–C44 n-alkanes, 2–6-ring PAHs	Dai et al. (2017); Gurav et al. (2017)
	Gordonia	C6, C8–C25 n-alkanes, branched alkanes, naphthalene, phenanthrene, thiophene, fluorene, chrysene, C21-triaromatic, pyrene, benz(a)pyrene	Brown et al. (2016); Kim et al. (2013); Qi et al. (2017)
	Micrococcus	C16–C36 n-alkanes, C6–C10 n-alkanes, phenanthrene	Al-Awadhi et al. (2007); Ghosh and Chakraborty (2020)
	Microbacterium	C18 n-alkanes, phenanthrene	Al-Awadhi et al. (2007)
	Mycobacterium	C11–C28 n-alkanes, branched alkanes, phenanthrene, fluoranthene, pyrene	Guo et al. (2010); Kotani et al. (2006); Nhi-Cong et al. (2009)
	Nocardia	C6–C16 n-alkanes, pristane, alkylbenzene, naphthalene	Le et al. (2010)
	Nocardioides	C8–C11 n-alkanes, phenanthrene	Brown et al. (2017); Saito et al. (2000)
	Rhodococcus	C6–C36 n-alkanes, phenathrene, anthracene, fluoranthene, chrysene, pyrene	Guo et al. (2010); Nhi-Cong et al. (2009); Song et al. (2011)
	Streptomyces	naphthalene, anthracene, Fluorene, phenanthrene, pyrene	Chaudhary et al. (2011); Gallo et al. (2012)
	Thermoleophilum	C13–C20 n-alkanes	Perry (2015)
Bacteroidetes	*Cytophaga*	Crude oil	McGenity (2019)
	Flavobacterium	PAHs, n-alkanes, mono-substituted alkylbenzenes	Turner et al. (2015); Zhang et al. (2012)
	Weeksella	C12–C34 n-alkanes, pristane, biphenyl	Wentzel et al. (2007); Yuste et al. (2000)
Firmicutes	*Bacillus*	C15–C36 n-alkanes, acenaphthene, fluoranthene, pyrene, benzo[e]pyrene	Feitkenhauer et al. (2003); Zhuang et al. (2002)
	Desulfosporosinus	PAHs, C4,C12 n-alkanes	Kleindienst et al. (2014); Liu et al. (2004)
	Dethiosulfatibacter	PAHs	Muangchinda et al. (2013)
	Geobacillus	C15–C36 n-alkanes, naphthalene	Sun et al. (2015b); Zheng et al. (2011)
	Lactobacillus	Crude oil	McGenity (2019)
	Paenibacillus	Naphthalene, phenanthrene, fluorene, fluoranthene, pyrene, benz(a)pyrene	Daane et al. (2002); Zhu et al. (2016)
	Peptococcus	Crude oil	McGenity (2019)
	Planococcus	C11–C33 n-alkanes	Engelhardt et al. (2001)
	Sarcina	Crude oil	McGenity (2019)
	Staphylococcus	Phenanthrene	Mallick et al. (2007)
Deinococcus	*Thermus*	C9–C39 n-alkanes, acenaphthene, fluoranthene, pyrene, benzo[e]pyrene, resins, asphaltenes	Feitkenhauer et al. (2003)

Aerobic degradation of oil pollutants

Aerobic degradation has a rapid pollutant conversion rate and relatively low requirements for environmental conditions. The process of molecular oxygen as the hydrogen acceptor plays a major role in the remediation of oil-contaminated shorelines.

Aerobic degradation of saturated hydrocarbons

Saturated hydrocarbons, which are mainly composed of n-alkanes, branched chain alkanes, and cycloalkanes, are the most easily degradable components in petroleum (Rojo 2009). The degradation of n-alkanes mainly includes pathways of terminal oxidation, sub-terminal oxidation, and double-terminal oxidation (Abbasian et al. 2015). For the terminal oxidation of n-alkanes, the methyl of n-alkanes is eventually oxidized to alcohols, aldehydes, and fatty acids with the aid of hydroxylase (oxygenase) and dehydrogenase; these fatty acids enter the tricarboxylic acid cycle through β-oxidation (Fig. 1). For double-terminal oxidation, one end of the fatty acid formed by terminal oxidation is oxidized to hydroxyl through ω-oxidation, and then further metabolized to dicarboxylic acid, before finally entering the tricarboxylic acid cycle through β-oxidation (Fig. 1). Sub-terminal oxidation is a series oxidation of n-alkanes to secondary alcohols, methyl ketones, acetyl esters and then acetyl esters, grade alcohol (acetate), and finally fatty acids catalyzed by hydroxylase (oxygenase) and dehydrogenase (Fig. 1). At the end, the fatty acids enter the tricarboxylic acid cycle through β-oxidation. The above hydroxylation processes are catalyzed by monooxygenase, while long-chain alkanes can be oxygenated by dioxygenase to form alkyl hydrogen peroxide, which can then be converted into fatty acids without passing through the Finnerty pathway of alcohol intermediates (Sakai et al. 1996).

The degradation pathway of branched alkanes is similar to that of normal alkanes. It starts at the end or sub-end of the long chain alkanes to form branched fatty acids and enters the TAC cycle through ω- or β-oxidation. However, the more branches and the longer chains, the greater the difficulty of degradation. Phytane and pristane with high branching degree and isoprenoid structure are the most difficult to oxidize and are often used as biomarkers (Abbasian et al. 2015).

Cycloalkanes, such as steranes and hopanes, with complex structures are usually the most persistent in the environment (Wang 2007). The degradation mechanism of the side chain of cycloalkanes is believed to be similar to that of the

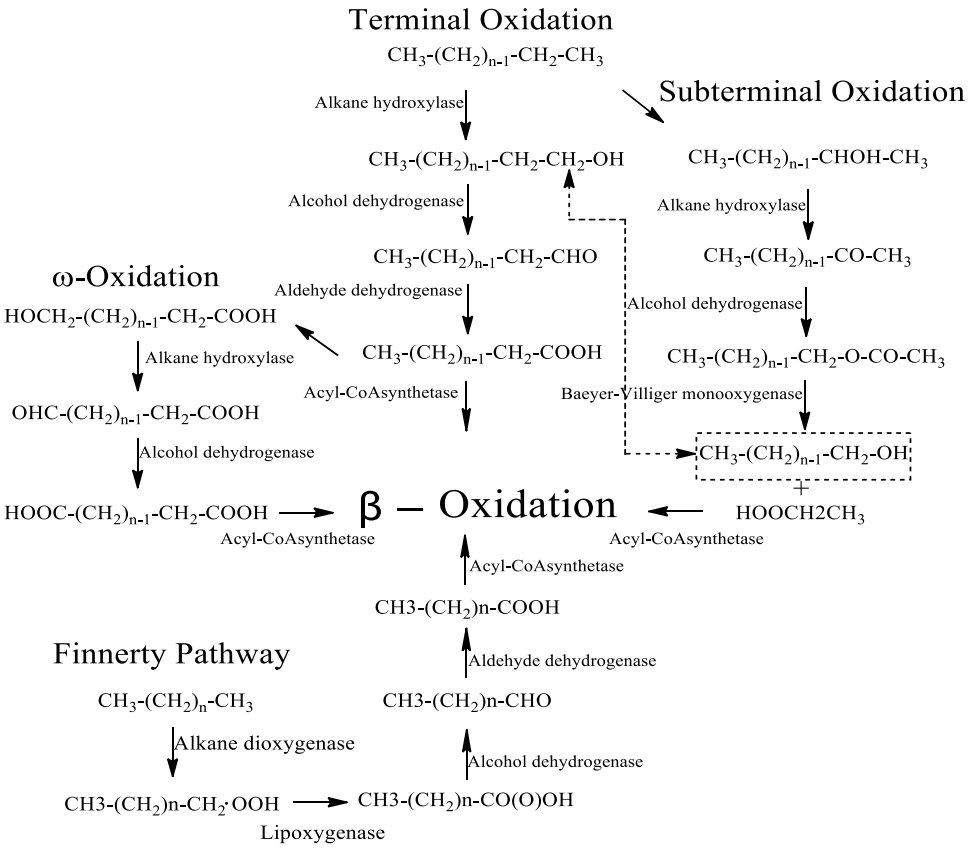

Fig. 1 Aerobic degradation pathways of n-alkanes

sub-terminal oxidation of n-alkanes. Cycloketones are first formed by the catalysis of oxygenase and dehydrogenase, and then by lactonization (Abbasian et al. 2015). One of the limiting factors for the degradation of cycloalkanes is that there are no individual microorganisms known to be able to oxidize these macromolecules to produce cyclic ketones for lactonization (Abbasian et al. 2015; Kostichka et al. 2001). Therefore, a synergistic effect of microbial communities is crucial for the successful degradation of cycloalkanes (Abbasian et al. 2015; Varjani 2017).

Aerobic degradation of aromatic hydrocarbons

Benzene, toluene, ethylbenzene, and xylene (BTEX) are the most widely studied monocyclic aromatic hydrocarbons (El-Naas et al. 2014). In the presence of dioxygenase, the benzene ring is hydroxylated to form cis-dihydrodiol, the cis-dihydrodiol ring is then broken to produce catechol, and catechol is further metabolized to form succinic acid and acetyl CoA (Fig. 2) and other intermediates of the TCA cycle (Juhasz and Naidu 2000). The metabolic intermediates generate formic acid, acetaldehyde, and pyruvic acid. Some studies have shown that higher pH favors the formation of succinic acid and acetyl CoA, while high C/N ratios tend to enhance benzene-ring opening pathways (El-Naas et al. 2014). Hydroxylation of the benzene ring catalyzed by dioxygenase is usually the rate limiting step of aromatic degradation, and oxygenase is the key enzyme to promote catalysis (Wang et al. 2018b).

The degradation of polycyclic aromatic hydrocarbons (PAHs) mainly depends on their structural properties and the adaptability of microbial degrading enzymes (Alegbeleye et al. 2017b). In terms of PAH degrading bacteria, *Rhodococcus* sp., *Sphingomonas* sp., *Pseudomonas* sp., and *Mycobacterium* sp. are the most widely studied (Brzeszcz and Kaszycki 2018; Nzila 2018). There are two main pathways for the microbial degradation of PAHs. Low molecular weight polycyclic aromatic hydrocarbons (LMWPAHs) with two or three benzene rings (Nzila 2018) by microorganisms as their carbon and energy sources to metabolize into CO_2 and H_2O for complete degradation (Mallick et al. 2011). High molecular weight polycyclic aromatic hydrocarbons (HMWPAHs) are generally highly resistant to biodegradation and can only be degraded by co-metabolism (Ghosal et al. 2016; Sivaram et al. 2019). However, the co-metabolites of HMWPAHs may be more biotoxic and have greater difficulty to achieving final mineralization (Maiti et al. 2012).

Degradation of LMWPAHs as single carbon and energy sources

Naphthalene and phenanthrene are the simplest PAHs, and their degradation mechanism has been thoroughly studied. Figure 3 shows a typical process of naphthalene degradation by bacteria (Habe and Omori 2003). Hydroxylation of the benzene ring is the initial step in the degradation of naphthalene, during which benzene combines with two oxygen atoms to form cis-naphthalene dihydrodiol by dioxygenase. Then cis-naphthalene dihydrodiol cleaves a benzene ring and converts it into salicylaldehyde and salicylic acid by a series of enzymes. Salicylic acid can be further converted into catechol or gentian acid by hydroxylase. Both intermediates can

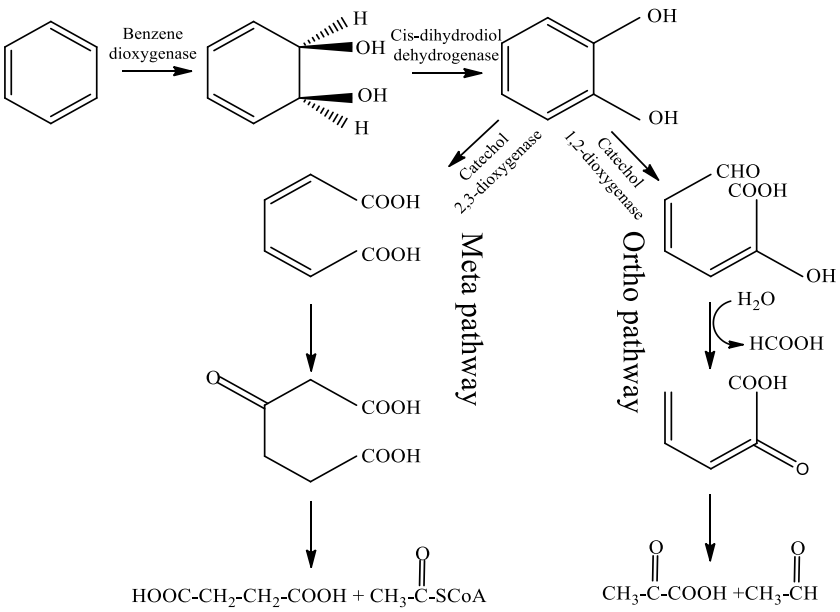

Fig. 2 Aerobic degradation pathways of monocyclic aromatic hydrocarbons

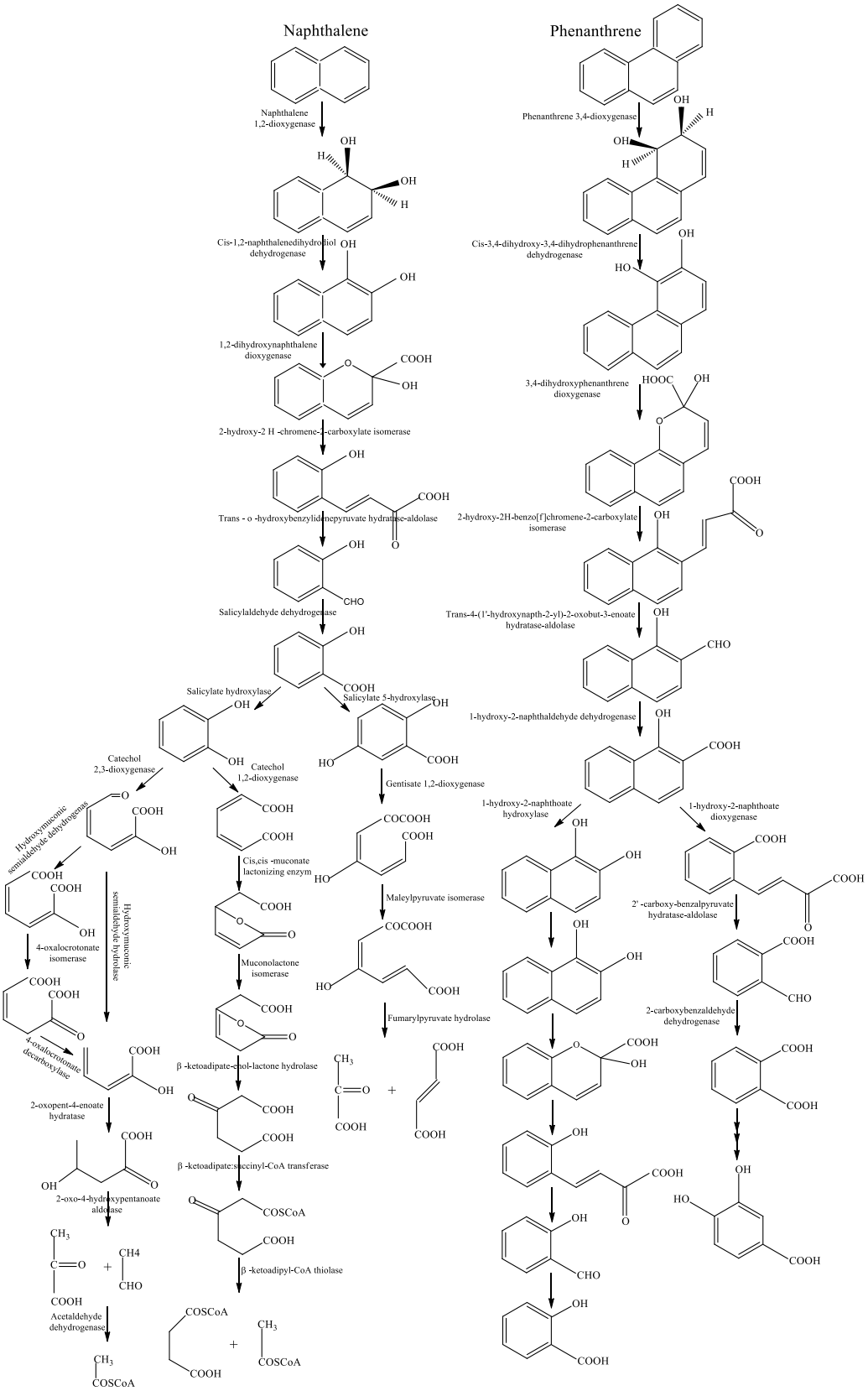

Fig. 3 Aerobic degradation pathways of naphthalene and phenanthrene (Mallick et al. 2011)

be metabolized into the TCA cycle, and finally be mineralized by the bacteria.

The "bay region" and "K region" are often considered the basic structural units of PAHs (Mallick et al. 2011). Phenanthrene is the smallest PAH with the above structure, and so it is often used as a model compound for study on the metabolism of PAHs. The most common degradation pathway of phenanthrene is shown in Fig. 3 (Mallick et al. 2011). Phenanthrene is hydroxylated at the 3,4 C position by dioxygenase, followed by a series of biochemical reactions, such as dehydrogenation, isomerization, and hydration, to cleave a benzene ring to produce 1-hydroxy-2-naphthoic acid. For some bacteria, such as *Pseudomonas* sp., 1-hydroxy-2-naphthalenecarboxylic acid may be converted into dihydroxynaphthalene, which is further degraded in a manner similar to naphthalene, using a salicylic acid pathway or naphthalene pathway. For microbes that cannot use naphthalene, 1-hydroxy-2-naphthoic acid is oxidized and cleaved by dioxygenase to form phthalic acid and protocatechuic acid, which then enter the TCA cycle. In addition, there are a few reports on the hydroxylation and ring cleavage of phenanthrene at the 1,2 C and 9,10 C sites, while some strains even have multiple degradation pathways (Mallick et al. 2011).

Co-metabolism of HMWPAHs

Co-metabolism is the phenomenon by which microorganisms have the sole carbon source as their co-substrate or primary substrate and also catabolize the secondary substrate; in contrast, these substrates cannot be used individually (Beam and Perry 1973). For example, *Pseudomonas saccharophila* p15 cannot use benzoanthracene and benzo[α] pyrene as carbon sources and energy sources for its growth, but when salicylic acid exists in the medium, it is able to oxidize and degrade both substrates (Chen and Aitken 1999). Similarly, when salicylic acid, phthalic acid, phenanthrene, or even light oil and glucose are used as co-substrates, *Pseudomonas* sp. and halophilic bacterial consortium have higher degradation rates of benzo[a]pyrene (Arulazhagan et al. 2014; Chen and Aitken 1999). Co-metabolism also exists in the degradation of refractory nitrogen-sulfur heterocycles and halogenated aromatic hydrocarbons in a soil/compost mixture (Meyer and Steinhart 2000).

Co-metabolic degradation has been widely reported, but its mechanism is yet to be fully explained (Zhang et al. 2019b). At present, the hypothesis of co-induction or "coenzyme effect" by nonspecific degrading enzymes has been accepted (Luo et al. 2014). Khara et al. (2014) reported that dioxygenase gene from *Sphingomonas* was transferred into *Escherichia coli* to enable the constructs to degrade more types of PAHs. With the existence of some substrates, the constructs were induced to produce dioxygenases for the degradation of HMWPAHs. These growth substrates were mostly LMWPAHs with similar structure or their degradation products (such as salicylic acid, phthalic acid, etc.) (Horvath 1972). Some studies have shown that conventional carbon sources, such as glucose and starch, can be used as the primary substrates for co-metabolism of refractory organic compounds (Luo et al. 2008), and their catabolism provides the necessary co-factors for PAH degradation. Owing to the complexity of biochemical and molecular mechanisms of microbial co-metabolism, the mechanisms need to be further studied and verified.

Anaerobic degradation of oil pollutants

It was long believed that O_2 was not only the final electron acceptor for microbial degradation of petroleum hydrocarbons but also an indispensable reactant. Lovley and Lonergan (1990) isolated the first Fe (III) reducing bacteria that could anaerobically degrade aromatic hydrocarbons as the sole carbon source. Since then, many anaerobic microbes for the degradation of petroleum hydrocarbon have been reported (Chakraborty and Coates 2004; Jaekel et al. 2015; Kniemeyer et al. 2007; Widdel and Rabus 2001b). These microbes use NO_3^-, SO_4^{2-}, CO_2, or Fe (III) as electron acceptors for anaerobic degradation. Their reaction rates are slow with strict environmental requirements; however, many refractory organic compounds and their toxic metabolites that are hardly treated under aerobic conditions can be completely degraded in anaerobic environments (Díaz 2004; Sherry et al. 2013).

For common NO_3^- and SO_4^{2-} reductions, the main anaerobic metabolism of the oil pollutants involved is fumarate addition, hydroxylation, methylation, and carboxylation (Widdel and Rabus 2001a), as shown in Fig. 4. Fumarate reaction, the main path of anaerobic degradation of oil hydrocarbons, is a process in which hydrocarbon carbon atoms cleave the double bond of fumarate to produce alkyl or aromatic fatty acids, depending on the C–H bond activation energy of the substrate (Kniemeyer et al. 2007; Meckenstock and Mouttaki 2011). It is generally considered that the optimal value for the reaction is 355–430 kJ/mol (Widdel and Rabus 2001a). The secondary terminal carbon sites of alkanes and alkyl side chains are more active within the above energy range, while the C–H bond energy of the benzene ring is higher (> 460 kJ/mol); therefore, it is more appropriate for the other three reactions (hydroxylation, methylation, and carboxylation) (Meckenstock and Mouttaki 2011; Weelink et al. 2010). Many studies have shown that some bacteria can hydroxyl benzene (the hydroxyl from H_2O or HO·) to phenol under the action of dioxygenase, and then undergo further carboxylation and β-oxidation to finally generate benzoyl-CoA (Weelink et al. 2010). In addition, under SO_4^{2-} reducing conditions, naphthalene may be degraded

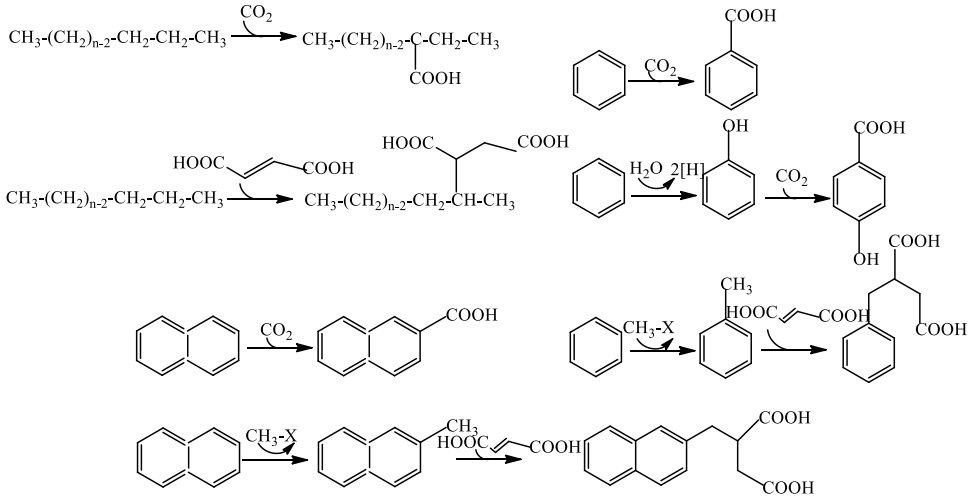

Fig. 4 Anaerobic degradation pathways of hydrocarbons

with the methylation reaction, while other petroleum hydrocarbons can obtain a carbon atom from CO_2\CO_3^{2-} and generate alkyl or aryl carboxylates (Rabus et al. 2016).

Key enzymes involved in microbial degradation

Although the microbial degradation of oil pollutants in shorelines involves both aerobic and anaerobic degradations, aerobic degradation is preferable owing to its faster reaction rate and stronger environmental adaptability. In aerobic treatment, the initial reaction step for the degradation of petroleum hydrocarbons is to add one or two hydroxyl groups to the hydrocarbon skeleton (Figs. 1, 2, and 3). The reaction is usually completed by the biocatalysis of monooxygenase or dioxygenase. Enzymes used depend on the molecular size of the petroleum hydrocarbons.

Alkane-degrading enzymes

The initial hydroxylation of alkanes can be accomplished by varying categories of monooxygenases (Table 3). The alkane hydroxylase from short chain alkane–degrading microbes is similar to methane monooxygenase. There are two different forms of methane monooxygenases: all methanotrophs produce a membrane-bound particulate form of methane monooxygenase (pMMO) that oxidizes n-alkanes in the C1–C4 range, while some methanotrophs additionally produce a soluble form (sMMO) that is active against a wider

Table 3 Enzymes for aerobic degradation of alkanes in bacteria

Enzyme	Hydrocarbon	Microorganism	Reference
sMMO, soluble methane monooxygenase	C1–C9 n-alkanes	*Pseudomonas* sp. *Gordonia* sp. *Mycobacterium* sp. *Pseudoocardia* sp.	Moreno and Rojo (2019)
pMMO, particulate methane monooxygenase	C1–C4 n-alkanes	*Methylomirabilis* sp.	Callaghan (2013)
Soluble cytochrome P450 (class I)	C5–C12 n-alkanes	*Acinetobacter* sp. *Mycobacterium* sp. *Rhodococcus* sp.	Funhoff et al. (2006)
Self-sufficient cytochrome P450 (class VII)	C14–C16 n-alkanes	*Dietzia* sp. *Alcanivorax* sp.	Minerdi et al. (2015)
AlkB-related	C5–C17 n-alkanes	*Pseudomonas* sp. *Mycobacterium* sp. *Rhodococcus* sp. *Burkholderia* sp. *Acinetobacter* sp.	Nie et al. (2014); Scheps et al. (2011); Schneiker et al. (2006); Sekine et al. (2006); Wang et al. (2010)
AlmA	C20–C36 n-alkanes	Acinetobacter sp.	Liu et al. (2011); Singh et al. (2012); Throne-Holst et al. (2007); Wang and Shao (2012)
LadA	C15–C36 n-alkanes	*Geobacillus* sp.	Feng et al. (2007)

range of substrates, oxidizing C1–C7 n-alkanes to the corresponding alcohols (Moreno and Rojo 2019). In general, *Pseudomonas butanovora*, *Gordonia* sp. TY -5, *Mycobacterium* sp. ty-6, and *Pseudoocardia* sp. ty-7 can all secrete monooxygenase to degrade short-chain alkanes (Moreno and Rojo 2019). Soluble cytochrome P450 and membrane oxygenase AlkB (integrated membrane non haem di-iron monooxygenase) are able to degrade C5–C17 (medium long chain) alkanes (Funhoff et al. 2006). P450s have been found in strains of *Acinetobacter*, *Mycobacterium* sp., *Rhodococcus* sp., and *Dietzia* sp., and in several Gram-negative bacteria including hydrocarbonoclastic bacteria such as *Alcanivorax* sp. (Nie et al. 2014; Scheps et al. 2011; Schneiker et al. 2006; Sekine et al. 2006; Wang et al. 2010). AlkB has been found in a variety of bacteria, such as *Pseudomonas putida* gpo1, *Mycobacterium tuberculosis*, *Rhodococcus rubrum*, *Burkholderia cepacia*, *Pseudomonas aeruginosa*, and *Acinetobacter* sp., among others (Singh et al. 2012). Long chain alkane–degrading enzymes include yellow binding monooxygenase (AlmA) and long-chain alkane monooxygenase (LadA) which are able to degrade alkanes with carbon chain length greater than C18. AlmA are able to oxidize C20 to > C32 n-alkanes (Throne-Holst et al. 2007). Genes homologous to almA have been identified in several other long-chain n-alkane–degrading strains, including *Acinetobacter* sp. M1 and several *Alcanivorax* species (Liu et al. 2011; Wang and Shao 2012).

LadA is expressed in *Geobacillus thermodenitrificans* NG80-2, which oxidizes C15–C36 n-alkanes, generating the corresponding primary alcohols (Feng et al. 2007). In general, an alkane-degrading bacterial strain can generate multiple alkane hydroxylases for the treatment of varying chain lengths of alkanes. *Pseudomonas aeruginosa* PAO1 can secrete two alkane hydroxylases, AlkB1 and AlkB2 (Rojo 2009). *Alcanivorax borkumensis* possesses two types of AlkB (AlkB1 and AlkB2), three cytochrome P450s (P450-1, P450-2, and P450-3), and one AlmA (Throne-Holst et al. 2007).

Polycyclic aromatic hydrocarbon degrading enzymes

The initial PAH is mainly completed by ring hydroxylating dioxygenase (RHD) (Zeng et al. 2017). RHD is a multicomponent enzyme, usually composed of two or three components, including oxygenase and electron transport chain (Kweon et al. 2008). Oxygenase is composed of an α subunit (α_n) or both α and β subunits ($\alpha_n\beta n$); α_n is a catalytic component responsible for electron transfer, while the βn subunit maintains the structural stability of the α-subunit (Kweon et al. 2008). Compared with alkane-degrading bacteria, PAH-degrading microbes have lower substrate specificity. The genes encoding the PAH oxygenase α_n subunit in Gram-positive bacteria are mainly distributed in three gene clusters: (1) nah-like, (2) phnAc-like, and (3) bphA1-like (Cebron et al. 2008). Most of these genes are located on the chromosome or plasmid DNA (Habe and Omori 2003) and are often detected in the bacteria *Sphingomonas* sp., *Burkholderia* sp., *polaromonas* sp., *Ralstonia* sp., *Comamonas* sp., *Marinobacter* sp., and *Pseudomonas* sp. (Cebron et al. 2008) Similarly, there are genes in Gram-negative bacteria that encode oxygenase like those described above. The gene-encoding PAH dioxygenases α_n in Gram-negative bacteria are mainly distributed in the following four gene clusters: (1) narA-like gene of *Rhodococcus* sp.; (2) nidA/pdoA1-like gene of *Mycobacterium* sp., *Nocardioides* sp., and *Mycobacterium* sp.; (3) phdA/pdoA2-like gene; and (4) nidA3/fadA1 of *Mycobacterium* sp. and *Terrabacter* sp. (Cebron et al. 2008). In addition to cyclohydroxylation dioxygenase, catechol dioxygenase is another key enzyme in the degradation process of polycyclic aromatic hydrocarbons. It can catalyze the intermediate metabolite pyrocatechol to carry out the meta and ortho cleavage, and promote complete ring opening of aromatic ring to produce the intermediate products of tricarboxylic acid cycle (Habe and Omori 2003). At present, studies have shown that xylE gene can encode catechol-2,3-dioxygenase synthesis (Song et al. 2017).

Microbial remediation technologies for oil-contaminated shorelines

Although the above factors impact microbial remediation of oil pollutants in the shorelines, many environmental factors cannot be easily adjusted to enhance pollutant degradation. For example, it is impractical to change the salinity and climate of the shorelines. Therefore, the study of feasible bioremediation enhancement strategies has become a research hotspot, and some research progress has been made in the four main aspects, as described below.

Oil-degrading microorganism-assisted microbial remediation

Oil pollution inevitably enables natural evolution of the marine microbial community (Khan et al. 2018). The bacterial populations are better able to tolerate and degrade pollutants via gradual accumulation to realize the environmental resilience (Liu et al. 2017a). However, the start-up of this process may be long, and indigenous populations are often unable to degrade all the oil pollutants (Shigenaka 2014). Addition of highly efficient oil-degrading microorganisms may be able to effectively solve the problems of indigenous populations with insufficient cell density, inhibited activity, and limited degradation ability. The forms of microorganisms so far applied include (i)

microorganisms indigenous to the polluted sites, (ii) exogenous microorganisms (either the pure culture of known microbial species/single strain or a collection of individual microorganisms to form a high-density cell mass (i.e., a microbial consortium), and (iii) genetically engineered microorganisms (recombinant microorganisms) (Nwankwegu et al. 2022). The type of microorganisms added often depends on the latest and historical knowledge of the contaminated site.

At present, a large number of efficient oil-degrading microorganisms have been applied, and many bioremediation agents have been commercialized. However, contrary to laboratory results, efficient degradation bacteria often fail in field tests or practical applications along the shorelines. For example, Venosa et al. (1992) tested 10 commercial bacterial agents during the Exxon Valdez oil spill, and only 2 showed a promotion effect on biodegradation when these products were disinfected, each group showed better degradation performance. This shows that indigenous microorganisms dominate the bioremediation process. In fact, exogenous strains can effectively exert their restoration process only when they have adapted to the physical and chemical conditions of the shoreline environment; only then can they compete with indigenous microorganisms for nutrients and avoid predation by protozoa (Mercer and Trevors 2011).

Immobilized microorganisms are used to resist the invasion of the unfavorable intertidal environment and competing indigenous microorganisms (Dai et al. 2022; Nhi-Cong et al. 2020; Partovinia and Rasekh 2018). The most common immobilization technique is formation of a biofilm or entrapment and encapsulation of microorganisms using polymeric gels (Partovinia and Rasekh 2018). The immobilization carrier provides a favorable micro-environment that helps microorganisms resist the invasion of the unfavorable intertidal environment and competing indigenous microorganisms (Hajieghrari and Hejazi 2020; Ruan et al. 2018). Furthermore, they enhance the activity, stability, and heavy oil biodegradation efficiency of inoculated microorganisms. The immobilization carrier can also loosen the shoreline sediments and increase oxygen flow (Tao et al. 2019), thereby accelerating microbial degradation of heavy oil. In our study (Dai et al. 2022), we used a modified zeolite immobilized bacterial consortium to remediate an intertidal zone polluted by heavy oil. After 100 days, the heavy oil degradation efficiency was 52.99%. Biochar, as an environmentally friendly material, offers great potential in the bioremediation of contaminated soils (Zahed et al. 2021) owing to its low cost, safety, and ability to maintain the activity of bacteria. Moreover, biochar also can improve the relative abundance and composition of indigenous oil-degrading microorganisms in sediments by serving as a high-quality carbon source, providing a microbial habitat, reducing nutrient loss, and adsorbing toxic hydrocarbons.

Nutrient-assisted microbial remediation

Nutrient addition is the most effective measure to maintain balanced microbial growth and is not toxic to the environment. Nutrients include carbon, nitrogen, phosphorus, and some other growth-limiting co-substrates (Gongora et al. 2022; Soleimani et al. 2013). Adding nutrient solution or solids is an effective way to improve the degradation efficiency of oil pollutants (Abou-Khalil et al. 2022). However, tides and waves along the shoreline environment are frequent, and nutrients are often washed out by seawater. Maintaining a high nutrient concentration in interstitial sediments is a problem that must be solved.

There are two main research directions with regard to this problem. The first is focused on beach hydraulics of nutrients and proposes an optimal nutrient addition strategy. The simplest dosing method is to spray the nutrient solution evenly on the beach surface at low tide. For example, a large number of spraying devices are arranged on the beach. However, this is costly and the high-salt seawater environment can easily cause devices to block. Other options are to dig ditches at the high tide water level and pipelines with holes to transport nutrient solution to the entire beach under groundwater activity during the tidal process (Venosa et al. 1996), or to slowly release lipophilic nutrients. The nutrients for slow release are usually in solid form, with hydrophobic materials such as kerosene, vegetable oil, or resin coated on the surface of inorganic nutrients to achieve controlled release of nutrients and overcome seawater scouring (Gallego et al. 2006). For instance, a slow-release nutrition capsule, Customblen, was used for the remediation of the Exxon Valdez oil spill. Vegetable oil was used as the coating material to contain calcium phosphate, amine phosphate, and ammonium nitrate (N: P: K = 28:8:0) (Swannell et al. 1996). The effect is most remarkable when it is combined with lipophilic nutrition agent Inipol EAP22, after which it can bind on the surface of oil pollutants and maintain an effective nutrient concentration of the oil–water interface for a prolonged time during biodegradation. Some studies have also suggested that this kind of lipophilic agent is more suitable for high-energy and coarse-grained sediment beaches compared with inorganic slow-release nutrients (Gallego et al. 2006). However, there still exist challenges for their application, including how to manipulate the release rate of slow-release nutrients and how to avoid competition by microorganisms to utilize lipophilic nutrients as carbon sources, which may inhibit degradation.

Biosurfactant-assisted microbial remediation

Biosurfactants have a good promoting effect on microbial degradation of oil pollutants. Biosurfactants help degradation by solubilizing or emulsifying oil pollutants (Liu et al.

2017b), increasing the interfacial uptake of oil pollutants by degrading bacteria (Zhong et al. 2014) or enhancing soil enzyme activity (Wang et al. 2018c). In addition, biosurfactants have the ability to weaken bacterial adsorption and enhance bacterial transport to or throughout the remediation sites (Zhong et al. 2017), which is of crucial importance for successful addition of efficient oil-degrading microorganisms for remediation.

Rhamnolipids are the most intensively studied biosurfactant. Owing to their advantageous physicochemical and biological properties, rhamnolipids are widely used in the field of oil pollution remediation (Karlapudi et al. 2018). The effects of rhamnolipids and Tween-80 on the degradation of phenanthrene by *Sphingomonas* gf2b have been studied (Pei et al. 2010). The phenanthrene biodegradation by *Sphingomonas* sp. GF2B was significantly inhibited (only 33.5% of phenanthrene degraded), while rhamnolipids significantly increased the degradation of phenanthrene (up to 99.5% of phenanthrene degraded). The authors proposed that rhamnolipids increase phenanthrene solubility, which is likely responsible for the high phenanthrene biodegradation efficiency in the presence of rhamnolipids. The effect of rhamnolipids on the biodegradation efficiency of diesel oil has also been (Kaczorek 2012). The results showed that presence of rhamnolipids significantly enhanced diesel oil degradation, giving rise to 88% loss after 14 days as compared with 44% loss with no surfactant presence. The authors found that rhamnolipids significantly increased the cell surface hydrophobicity of *Pseudomonas stutzeri* AG 22 as compared with two other surfactants. In another study, the field-scale bioremediation of PAH-contaminated farmland soil from the Shenyang North New Area of China was investigated using the bacteria *Arthrobacter globiformis* with addition of different concentrations of rhamnolipids (Wang et al. 2018c). The optimum rhamnolipid concentration of 5 mg/kg resulted in a PAH removal rate of 35.6% at 150 days. This was 29.3% higher than that of the control (no rhamnolipids and *Arthrobacter globiformis*), 19.8% higher than the rhamnolipid treatment alone (5 mg/kg), and 13.8% higher than the *Arthrobacter globiformis* treatment alone. The authors concluded that rhamnolipids enhanced soil catalase, invertase activities, and *Arthrobacter globiformis* reproduction during the PAH biodegradation processes. However, there still exist challenges for rhamnolipid application, such as how to avoid blocking effects and how to be degraded by microorganisms to provide a carbon sources.

Enzyme-assisted microbial remediation

Enzyme remediation has been considered an ideal remediation strategy for intertidal oil pollution since it requires neither nutrition from the environment nor the prevention of predators and toxic substances. Moreover, it overcomes the limitation of slow rate of degradation exhibited by microorganisms (Dai et al. 2020; Gaur et al. 2021). In addition, enzyme remediation also has the advantages of playing a role in different pollutant concentrations, low energy input, reducing sludge generation, and high specific rapid biodegradation (Mishra et al. 2020). Catalase, lipase, and oxidoreductase, which include monooxygenase, dioxygenase, alcohol dehydrogenase, and alkane hydroxylase, play important roles in the degradation of hydrocarbons (Suganthi et al. 2018). Lipase catalyzes the hydrolysis of crude oil components into simple compounds that can be used by microorganisms, while catalase decomposes hydrogen peroxide into oxygen and water, which reduces the oxidative stress caused by hydrocarbons (Achuba and Okoh 2014). Oxidoreductase can catalyze the oxidation and reduction of toxic hydrocarbons into simpler components (Suganthi et al. 2018).

The removal effects of catalase, lipase, and oxidoreductase on petroleum hydrocarbons in oil sludge have been studied. A bacterial consortium (composed of *Shewanella chilikensis*, *Halomonas hamiltonii*, and *Bacillus firmus*) was able to degrade 96% of total petroleum hydrocarbon by producing enzymes such as 46 U/mL catalase, 68 U/mL oxidoreductase, and 80 U/mL lipases (Suganthi et al. 2018). In our study, the immobilized laccase-bacteria consortium system was also used to remediate a shoreline polluted by heavy oil (Dai et al. 2020). The degradation efficiency of the immobilized laccase-bacteria consortium for heavy oil was 66.5% after 100 days of remediation, with a reaction rate constant of 0.018 day^{-1}. Moreover, immobilized laccase was found to rapidly decompose polycyclic aromatic hydrocarbons with high petroleum toxicity (Kucharzyka et al. 2018) and promote the growth and reproduction of heavy oil–degrading bacteria. The use of enzymes to degrade oil pollutants can quickly reduce biological toxicity and initiate the biodegradation of oil pollutants.

Influencing factors of microbial remediation of oil-contaminated shorelines

Microbial degradation is the main method for removing oil pollutants from shorelines. Bioremediation of the shorelines is mainly affected by physical and chemical properties, biodegradability, bioavailability of oil pollutants, and microbial degradation capacity. In addition, environmental factors (sediment properties, temperature, nutrients, oxygen, electron acceptor, salinity) also impact microbial remediation in shorelines. Effective bioremediation strategies need to take into account all the above factors.

Properties of oil pollutants

The physical and chemical properties and bioavailability of oil pollutants play a vital role in the effectiveness of bioremediation (Ma et al. 2015). The biodegradability of oil components is ranked in the following order: straight chain alkanes > branched chain alkanes > low molecular weight alkyl aromatics > monocyclic aromatic hydrocarbons > cycloalkanes > PAHs > resins > asphaltenes (Varjani and Upasani 2017). Oil pollutants in high concentration often have strong biotoxicity, which can not only inhibit the growth and metabolism of microorganisms but also limits the mass transfer of nutrients and O_2 (Al-Hawash et al. 2018). However, a low pollutant concentration can also affect bioremediation because the microbial population may struggle to survive without sufficient carbon sources (Varjani and Upasani 2017). Bioavailability is the amount of substances that microorganisms can obtain through physical and chemical mechanisms. Increasing bioavailability is an effective pathway to improve the efficiency of bioremediation (Varjani and Upasani 2016). A large number of studies have shown that the addition of surfactants can increase the bioavailability of oil pollutants and improve bioremediation efficiency (Karlapudi et al. 2018; Kleindienst et al. 2015; Xu et al. 2018). There is increasing interest in the application of microbial surfactants over chemical surfactants owing to (a) relative nontoxicity and high biodegradability (Varjani and Upasani 2016a), (b) unique structural properties for application in environmental clean-up (Zhao et al., 2016), and (c) high selectivity and specific activity at harsh environmental conditions (e.g., temperature, pH, and salinity) (Varjani and Upasani 2016b).

Microbial community

The composition of oil pollutants is extremely complex, and a single type of microorganism will often have limited ability to degrade specific components in crude oil (Acosta-Gonzalez and Marques 2016). For example, *Alcanivorax* sp. is a common obligate alkane-degrading bacteria, while *Cycloclasticus* sp. and *Marinobacter* sp. are often reported as PAH-degrading bacteria (Head et al. 2006). For a single oil pollutant, its biodegradation is usually carried out step by step with the participation of various enzymes or microorganisms (Figs. 1, 2, 3, and 4). Therefore, the degradation of crude oil requires the cooperation of a variety of petroleum-degrading microorganisms. The species, quantity, and community structure of microorganisms in the sedimentary environment have important impacts on the remediation effect.

Oil pollution is also a process of acclimation and selection of environmental microorganisms (Shaoping et al. 2021; Abou-Khalil et al. 2023). Microbial populations that can adapt to the polluted environment or have pollutant-degradation enzymes gradually enrich to perform selective succession with the changing composition of the oil pollutants, which will ultimately realize the gradual removal of various types of oil pollutants (Head et al. 2006; Vila et al. 2010). It is of great significance to elucidate the complex synergistic mechanism of oil-degrading bacteria, and dynamic relationships between changes of oil components and changes of microbial community structure and metabolic function in the process of degradation.

Environmental conditions in the shorelines

Temperature

The ambient temperature along the shorelines affects the viscosity, toxicity, solubility, and volatility of the spilled oil, and composition/bio-availability of the pollutants, and the growth and reproduction, metabolic activity, the oil pollution degradation rate of microorganisms (Megharaj et al., 2011). Increasing temperature increases the solubility of hydrophobic pollutants, decreases viscosity, and enhances diffusion and transfer of long chain n-alkanes from solid phase to water phase. At low temperatures, the viscosity of oil increases, volatilization of toxic short-chain alkanes is reduced, and their water solubility is decreased, which delays the onset of biodegradation (Aislabie et al. 2006). The optimal oil degradation temperature in an aerobic environment is 15–40 °C, and in the marine environment is ~ 20–30 °C (Al-Hawash et al. 2018). In open environments, the temperature fluctuation range, frequency, and duration vary with place and season, resulting in different restoration effects.

Nutrients

Availability of nutrients is important for successful oil biodegradation, including nitrogen, iron, and phosphorus in some cases. After an oil spill, the carbon source (petroleum hydrocarbons) in seawater and sediments increases greatly, and nutrients (e.g., N and P) become the limiting factor for biodegradation. Therefore, supply of nutrients for environmental microorganisms is an effective pathway to improve the efficiency of bioremediation, while the type, concentration, and ratio of nutrients should also be effectively controlled (Varjani et al. 2014). Excessive amounts of nitrogen in soil cause microbial inhibition. Maintaining nitrogen levels below 1800 mg nitrogen/kg H_2O leads to optimal biodegradation of hydrocarbon pollutants (Walworth et al. 2007). Excessive nutrient concentrations, especially NPK, inhibit the biodegradation activity of hydrocarbon pollutants (Varjani 2017).

Oxygen

Alkanes and most aromatics generally require an oxygen supply for aerobic bioremediation. For example, in the bioremediation of the Exxon Valdez oil spill in the USA, many failed field study and practice cases could be attributed to the lack of oxygen in the sediment (Ramsay et al. 2000). On the surface of seawater, in the upper sediment layer, and in other areas exposed to waves and tidal currents, O_2 is not a limiting factor. However, in fine sand beaches, muddy tidal flats, wetlands, swamps, and lower sediments conditions of most shorelines, the mass transfer of O_2 is often insufficient for the consumption of microorganisms, which is thus considered the limiting step of bioremediation (Mercer and Trevors 2011). The O_2 availability of sediments can be improved by applying oxygen generators (H_2O_2, CaO_2) or mechanical means (e.g., compressed air supply) (Ramsay et al. 2000). Although some refractory oil pollutants can be completely degraded under anoxic and anaerobic conditions with NO_3^-, SO_4^{2-}, CO_2, or Fe (III) as electron acceptors (Meckenstock et al. 2016), the anaerobic degradation rate is much lower than that of the aerobic process. As such, it is only applicable in the low energy, fine, and its underlying sedimentary environment with insufficient O_2 mass transfer.

pH

Seawater is usually slightly alkaline, but sediment pH can vary significantly. Organic matter increases acidity; the pH of swamp sediments can reach as low as 5.0, while mineral soil and sediment are neutral or slightly alkaline (Venosa and Zhu 2003). The acid-base environment of sediments has a significant influence on microbial activity and the availability of pollutants and nutrients (Obahiagbon et al. 2014). Most bacteria are suitable for degradation of oil pollutants in near neutral or slightly alkaline environments. This is also why bioremediation is difficult for oil pollution in marsh, mangrove, and other wetland systems (Mercer and Trevors 2011).

Salinity

High salinity is an important factor limiting the biodegradation of oil pollutants in the shoreline (especially in the supratidal zone and upper intertidal zone). Salinities can increase up to 160 g/L or even

higher in the supratidal zone and upper intertidal zone owing to the evaporation of seawater (Geng and Boufadel 2017). (Abou Khalil et al. 2021b) have shown that as salinity increases, the biodegradation of petroleum hydrocarbons by indigenous marine oil–degrading microorganisms decreases, with a decrease of two times at a salinity of 90 g/L and a decrease of four times at a salinity of 160 g/L. Furthermore, further research has shown that salinity has a significant impact on the biodegradation of aromatic hydrocarbons, while it has no significant impact on the biodegradation of alkanes (Abou Khalil et al. 2023). Various salt-tolerant and halophilic microorganisms with petroleum degradation ability have been screened to solve the above problems (Gibtan et al. 2017). In addition, salinity is also an important parameter affecting the cycle and migration of nitrogen and phosphorus in coastal sediments (Wang et al. 2018a).

Sediment properties

The migration and transformation of oil spill pollutants in sediments and pores, which are controlled by sediment, waves, and tidal conditions along the shoreline, determine the growth conditions of microorganisms (Wang et al. 2020b). Compared with fine beaches, oil pollutants are more likely to the penetrate deep sediments of coarse beaches and remain long term as they cannot be washed by waves (Boufadel et al. 2019); therefore, the larger the sediments grain sizes, the more sensitive they are to oil spill pollution (Southam et al. 2001). The O_2 concentration of deep sediments is limited, and the biodegradation rate is relatively slow. In addition, waves, tidal currents, and oil exposure can significantly affect the removal of oil pollutants. For example, rocky coastlines exposed to waves and tidal currents are the least sensitive environments to oil spill pollution and human activities, and can be naturally restored after several months (Boufadel et al. 2019). Moreover, mechanical and chemical measures can accelerate the recovery speed. However, since both material flow and biological flow are controlled by physical scouring process, bioremediation is challenging. In contrast, loose and sheltered shoreline sediments (e.g., swamp, mangrove) with no waves or weak waves are very sensitive to oil spill pollution (Wang et al. 2020b). The pollutants usually stay for several years and mechanical and chemical treatments are likely to aggravate ecological damage. In these shoreline environments, bioremediation is often the most cost-effective method.

Limitations and future research directions

Although microbial remediation agents for shorelines have been repeatedly demonstrated in laboratory, they often fail in the field environment. In the shoreline environment, oil-degrading microorganisms (endogenous and exogenous) that were highly efficient in the laboratory may not be able to adapt to physical and chemical conditions to compete with the indigenous ecology. Moreover, they often need to go through a long start-up period. Under the unique hydrodynamic conditions of the shorelines, powder or

solid based agents are easily diluted by seawater erosion, resulting in high failure rates. In addition, microorganisms preferentially degrade certain oil components, resulting in the accumulation of long-chain alkanes, polycyclic aromatic hydrocarbons, and other refractory components in the environment. This eventually increases the toxicity of the microenvironment, inhibiting the microbial growth and metabolic activity, leading to excessively long microbial remediation time. In addition, microbial remediation may also fail owing to uncontrolled environmental parameters (e.g., temperature, pH, and salinity) which are essential for optimum activity of microorganisms. Further research is needed to enhance the environmental adaptability of microbial remediation technologies.

Another perspective to consider in the future is sustainable microbial remediation technology of oil contaminated sediments. This will require effective multidisciplinary collaboration between researchers working in microbiology, environmental geochemistry, materials science, and engineering. New and sustainable microbial remediation technologies and low-carbon remediation materials should be further developed to meet the growing demand for sediment remediation. In addition, advanced characterization methods should be used to deepen understanding of the microbial degradation mechanism and promote the development of new microbial remediation technologies. The combined application of life cycle assessment, environmental impact assessment, cost-benefit analysis, and other methods to evaluate the feasibility of sustainable microbial remediation technology should also be carried out.

Conclusions

Oil pollutants have serious adverse impacts on the ecology of shoreline environments. Oil-degrading microorganisms can be used to degrade oil pollutants. Catabolic pathways involved in biodegradation reveal efficient strategies for oil pollution microbial remediation. Understanding key enzymes of oil microbial degradation is of great research interest to accelerate biodegradation. Optimizing the influencing factors will improve the efficiency of microbial remediation. Sustainable microbial remediation technology is the key to microbial remediation of shoreline oil pollutants. Addressing the limitations of microbial remediation technologies for shoreline oil pollution should be the focus of future research.

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